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A global assessment of the potential distribution of naturalized and planted populations of the ornamental alien tree *Schinus molle*

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Abstract

The Peruvian Peppertree (*Schinus molle* L.) is an evergreen tree native to semiarid environments of Peru and Bolivia in South America. This tree has been introduced and widely planted for ornamental and forestry purposes in several semiarid regions of the world because its seedlings are easily established and have a high survival rate; it also grows quickly, and it is tolerant of dry climates. We compared the global and regional niches of naturalized and planted populations of *S. molle* in order to examine the invasive stages and potential distribution of this species in four regions of the world. This work provides a novel approach for understanding the invasion dynamics of *S. molle* in these areas and elucidates the ecological processes that bring about such invasions. Most naturalized and planted populations were found to be in equilibrium with the environment. In its native range as well as in Australia and South Africa the models of the coverage area of habitat suitability for natural populations were the highest, whereas the coverage area of planted populations was lower. For planted populations in Australia and South Africa, a large percentage of predicted presences fell within sink populations. The invasion stages of *S. molle* vary across regions in its adventive range; this result may be attributable to residence time as well as climatic and anthropic factors that have contributed to the spread of populations.

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Keywords
Global niche, niche conservatism, plant invasions, regional niche, stage of invasion, tree invasions

Introduction

Climate change has contributed to shifts or modifications of some tree species´ geographic distributions in recent decades (Hoffman and Sgrò 2011; Urban et al. 2016). Further range shifts (reductions and expansions) of many more species are expected in the coming decades, leading to a major reorganization of ecological communities and, potentially, biodiversity loss (Early and Sax 2011; Radchuk et al. 2019). Invasive species are a major component of global change and threaten native species and ecosystem integrity (Pyšek et al. 2020). Biological invasions have impacted ecosystems in many ways, including through hybridization with native species, effects on ecosystem processes, population dynamics, and by modifying of community structure and composition (Vilà et al. 2011; Vilà and Hulme 2017). Trees are increasingly important as invasive species in many regions of the world and have major impacts in such areas (Richardson et al. 2014; Rundel et al. 2014).

An example of a major invasive species is the Peruvian Peppertree (*Schinus molle* L.), a native tree of the Andes in South America (Ramírez-Albores et al. 2020), which has also been introduced, planted, and naturalized in several regions of the world (Taylor 2005). It is evergreen, fast-growing, drought- and -heat resistant, and has been introduced mainly to cities, towns, villages (in parks, gardens, and sidewalks), and farms as an ornamental tree, as well as along drainage lines, water bodies (rivers, streams, dams), agricultural fields (as shade trees, windbreaks, or hedgerows) and roads as an amenity. The successful introduction of *S. molle* in non-native ranges is attributed to its high drought-and-heat tolerance, its ability to compete for nutrients and light, its fast growth rate, and its prolific seed production (Iponga et al. 2008, 2009; Zahed et al. 2010). For these reasons, it has recently expanded its range considerably (Rouget et al. 2004; Iponga et al. 2008; Ramírez-Albores and Badano 2013; Rejmánek and Richardson 2013). Understanding which factors encourage the progress of the introduction-naturalization-invasion continuum is important when seeking measures to manage the invasive species' effects on native biota (Richardson et al. 2000; Pyšek and Richardson 2006; Richardson et al. 2014).

One way of assessing whether evolutionary changes have occurred in an invasive species is to compare the climatic niche between its native distribution range to that of an introduced distribution range. Such studies assume that the niche of a species is formed by a series of vectors, each representing an environmental condition, the magnitudes of which define the range of conditions within which a species can exist (Soberón and Peterson 2011). Thus, if the magnitudes of the vectors that comprise a niche are similar in the native and introduced ranges, it can be concluded that the requirements of the species have not changed. In other words, this situation indicates that the species retains its niche in the introduced range, and therefore will colonize only sites with similar environmental characteristics to those that exist in their native

range (Soberón and Peterson 2011). However, if significant differences are detected in the magnitude of the vectors of the niche between native and introduced ranges it can be concluded that the species is being, or has been, shaped by selective pressures within the introduced range (Soberón and Peterson 2011).

In this sense, Gallien et al. (2012) proposed that invasion processes could be inferred by comparing the outputs of global and regional niche models. The global model can be constructed using all occurrence records for the species climatic spaces worldwide. Meanwhile, the regional model, captures all the abiotic and biotic conditions that the species occupies in its native or invaded range. Knowledge of the species' populating stages during invasion has the potential to provide important insights into the future dynamics and potential threat of an invader (Roura-Pascual et al. 2009; Gallien et al. 2012). For instance, many naturalized species occupy climatic conditions that are more extreme than the conditions found in their native range (Broennimann et al. 2007; Gallagher et al. 2010; Petitpierre et al. 2012; Sax et al. 2013). Although in the realized niche, some invasions and survival in situ beyond conditions in the distribution could be the result of evolutionary change, it is likely that some cases prevail because conditions in the native distribution represent only a subset of the existing fundamental niche of the species (Buswell et al. 2011; Sax et al. 2013). Another reason for this is that human actions substantially change environmental factors, e.g., through disturbance, irrigation, or nutrient addition, thereby totally altering and rendering invalid any correlations between occurrence and environmental factors (González-Moreno et al. 2015; Walker et al. 2017). The latter case seems particularly likely for naturalizations of long-lived species such as trees, where there has typically been limited time for evolutionary change in recently established populations (Sax et al. 2013).

This study focuses on the modeling and comparison of the regional and global climate niches of *S. molle*). The long residence time and large extent of plantings and invasion of *S. molle* across multiple regions make this a good species for such a study. This comparison allowed us to infer the stage of invasion for *S. molle* and to determine which sites are most susceptible to invasion by this species. We hypothesize that there will be a differentiation between models (regional and global models) generated within a climatic niche if this species has responded to local selective pressures in *S. molle* naturalized populations (i.e., populations in natural environments without human subsidization) or planted (i.e., planted populations in urban or rural environments where their occurrence is at least partly attributable to human actions) within its introduced range.

Materials and methods

Study species

Schinus molle is native to semiarid Andean ecosystems of Peru and Bolivia and has been introduced to several regions of the world as an ornamental in human settlements as well as for forestry purposes as hedgerows and windbreaks in rural areas (Ramírez-Albores et al. 2016, 2020). Peppertrees recently began colonizing abandoned agroeco-

systems (Ramírez-Albores et al. 2016, 2020; Guerra-Coss et al. 2021). In addition to the several countries where populations have already been established (Iponga et al. 2008, 2009; Ramírez-Albores et al. 2016), *S. molle* has the potential to invade other semiarid environments (Iponga et al. 2008; Ramírez-Albores et al. 2020) in tropical and temperate regions (Milton et al. 2007; Guerra-Coss et al. 2021).

Occurrence data

Occurrence records of *S. molle* were obtained from our own fieldwork (in Mexico and South America) and were complemented with global occurrence data from scientific collections (see Suppl. material 1: Table S1), as well as literature and online sources. The references that report of the occurrence of *S. molle* without clear evidence of establishment were not included in the dataset (Table 1). Occurrence data records were grouped into (*i*) "naturalized populations" (i.e., individuals occurring in natural environments where they were not reliant on human nurturing), and (*ii*) "planted populations" (i.e., individuals that occur in urban and rural zones where their occurrence is potentially subsidized by human activities). Because sampling of occurrence data is commonly biased in favor of easily accessible areas, spatial data may not be completely independent. This can affect the performance of species distribution models (SDMs), which could lead to misinterpretations of models (Boria et al. 2014; Regos et al. 2019).

Bioclimatic variables

Environmental parameters were obtained from the WorldClim database (available at https://www.worldclim.org/). We used the altitudinal layer and bioclimatic variables pertaining to temperature and precipitation with a spatial resolution of 2.5 minutes (about 5 km^2). We performed a principal component analysis (PCA) and selected the subset of variables that were most strongly associated with the first two principal axes of ordination (Table 2). Collinearity between bioclimatic variables was reduced by eliminating highly correlated variables (Pearson correlation values ≥ 0.70) (Beaumont et al. 2005). We ran models with combinations of minimally correlated variables. Using these criteria, we selected 11 variables for the SDMs: altitude, mean diurnal range, isothermality, annual mean temperature, mean temperature of wettest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of driest month, precipitation seasonality, precipitation of warmest quarter and precipitation of coldest quarter. ArcGIS 10.2 was used to process the environmental layers (ESRI 2014).

Table 1. Date of first record and number of data records of Peruvian Peppertree (*Schinus molle* L.) in study regions.

	Global	Australia	California	Mexico	South Africa	Native region
Date of first record	–	1860	1650–1750	1540–1550	1880	–
Naturalized populations	905	62	23	128	19	81
Planted populations	1022	219	64	649	189	76

Table 2. Contribution (%) of the bioclimatic variables selected for the global and regional Peruvian peppertree (*Schinus molle* L.) distribution models.

	Model											
Variable	**Global** Planted	**Global** Naturalized	**Australia** Planted	**Australia** Naturalized	**California** Planted	**California** Naturalized	**Mexico** Planted	**Mexico** Naturalized	**South Africa** Planted	**South Africa** Naturalized	**Native region** Planted	**Native region** Naturalized
Altitude	0.8	0.4	14	2.7	10.1	5.1	26.2	13.1	28.6	7	19.8	40.8
Annual mean temperature	36.9	34.2	10.3	25.9	2.1	6.6	1.6	4.2	15.1	7.4	24.1	20.8
Mean diurnal range	2	0.2	2.9	2.9	6.5	0	1.2	1.2	0	4.1	0.4	0
Isothermality	47.7	58.4	3.5	0.4	4.2	21.4	24.3	19.3	0	2.1	4.4	6.5
Temperature annual range	6.4	0.7	1.9	6.8	11.7	30	6.3	4.3	8	2	5.2	2.6
Mean temperature of wettest quarter	0.3	0.6	3.8	19.3	22.4	1.8	4.5	21.5	7.2	5.7	0	0
Annual precipitation	0.7	1.2	5	6.6	9.1	12.2	13.3	15.5	0	1.2	1.9	3.1
Precipitation of driest month	0.8	1.1	16.3	16.7	6.6	9.7	3.7	1.3	6.7	21.7	1.3	0.8
Precipitation seasonality	0.4	0.1	3.8	4	14.4	1.7	2.1	10.2	0.4	6.4	3.8	2.8
Precipitation of warmest quarter	0.9	0.2	3	4.5	4.7	2.5	7.7	5.7	16.1	33	1.5	0.7
Precipitation of coldest quarter	3.2	2.4	35.4	10.3	8.2	8.9	9.1	4.6	17.8	9.4	37.6	21.8

Regional and global distribution models

The occupied climate space was compared between the native and invaded ranges using direct climate comparisons and PCA before ecological niche modeling; this allowed us to make a quick assessment of the relative positions of populations in climate space, using the 11 selected bioclimatic variables. A kernel function was used by converting the presence points to density values (Broennimann et al. 2012).

We then compared the regional versus the global niche range to assess whether the *S. molle* niche differed. To compare the distribution models, we projected the potential distribution from the regional niche and compared it with the potential distribution projected from the global niche (Medley 2010). To compare the global (where the invader species could spread) and the realized regional niches (where the invader species is already observed) we followed the framework proposed by Gallien et al. (2012). This framework allows us to infer both the stage of invasion for each population in the niche space and the degree of regional range filled by the invading species in geographical space. According to this framework, which was applied analytically by Kumar et al. (2015), if the regional and global niche models predict probabilities higher than 0.5 for the presence of the species, the species is in quasi-equilibrium (i.e., the populations are in a stabilizing stage). In contrast, if both niche models predict probabilities lower than 0.5 for presence of the species, this means that the locations may represent population sinks (i.e., sink populations). If the probability of presence of the species is higher than 0.5 in the global niche but in the regional niche the probability is lower than 0.5, this finding suggests colonization from different sources, including areas already invaded in the regional invaded range (i.e., populations colonizers). In contrast, if the probability of presence of the species is higher than 0.5 in the regional niche, but lower than 0.5 in the global niche, populations may be adapting to new environmental conditions (i.e., locally adapted populations). All analyses were performed in R (R Development Core Team 2019) using functions as ecospat and SDMtools (Broennimann et al. 2012; Di Cola et al. 2017).

We used MaxEnt (v.3.4) to construct the regional and global models of *S. molle.* MaxEnt computes the probability distribution of maximum entropy for the set of climatic variables with the occurrence records of the target species, but this procedure is constrained by the incomplete knowledge of the distribution of the species (Phillips et al. 2006; Graham et al. 2008; Elith et al. 2011). The resulting model is then a geographical projection of habitat suitability for the target species (i.e., probability for finding the species) where values close to 0 indicate sites that do not match with the niche requirements of the species, and values close to 1 indicate sites that fully match their niche requirements. Although other computer programs have also been used to model species climatic niches, several authors have shown that MaxEnt usually performs better when presence-only data are available (Graham et al. 2008; Elith et al. 2011). This produced a model of a suitable habitat for the species based on the climatic variables, expressed as a probability distribution (Phillips et al. 2006). Each niche model was calibrated with a random selection of 75% of the occurrence points

used as training data; the remaining 25% of the points were used as test data to validate the models. All models were regularized, modifying the value of the β parameter to avoid over-parametrization (only models with $\beta \cong 1$ were retained), therefore selecting the most conservative models (i.e., those with the best compensation between complexity and predictive capacity; Phillips et al. 2006; Peterson et al. 2011). For each model, we created 100 replicas considering a cross-validation approach in which the occurrence points are repeatedly split into two subsets: one for training and one for testing. Model performance was evaluated using the area under the curve (AUC) and partial ROC test (pROC) (Barve 2008; Peterson et al. 2008). Our product consisted of a projection (continuous map) of the habitat suitability for *S. molle* in the invaded range (Mexico, California, South Africa, and Australia). According to the predicted habitat suitability (Pachauri et al. 2014), four types of potential habitat suitability for *S. molle* were defined as follows: high suitability (>0.60), medium suitability (0.40–0.60), low suitability (0.20–0.40), no suitability (<0.20) (Pachauri et al. 2014). ArcGIS 10.2 (ESRI 2014), which was used to visualize and interpret the output in raster format.

Results

For all models, factors related to temperature were more important than those related to precipitation. The variable that contributed most strongly to the global models was isothermality followed by annual mean temperature (Table 2). For the regional models, the variables fluctuated, with the altitude, isothermality and precipitation of coldest quarter emerging as the most important (Table 2). All of the models had a good performance, with AUC values ranging from 0.758 to 0.973, and pROC values from 1.75 to 1.92: Global $_{planted}$ (AUC = 0.924 ± 0.001), Global $_{naturalized}$ (AUC = 0.952 ± 0.002); and Native region $_{planted}$ (AUC = 0.971 ± 0.03), Native region $_{naturalized}$ (AUC = 0.952 ± 0.04) (Table 3).

Table 3. Areas of calibration and performance statistics for naturalized and planted populations models of Peruvian peppertree distribution.

Model	Boyce index (β)	Test AUC	pROC
Global $_{planted}$	0.98	0.924 ± 0.001	1.91 ± 0.002
Global $_{naturalized}$	0.99	0.952 ± 0.002	1.90 ± 0.003
Australia $_{planted}$	0.99	0.927 ± 0.017	1.91 ± 0.030
Australia $_{naturalized}$	0.99	0.949 ± 0.005	1.85 ± 0.001
California $_{planted}$	0.99	0.932 ± 0.014	1.91 ± 0.030
California $_{naturalized}$	0.99	0.958 ± 0.014	1.85 ± 0.001
Mexico $_{planted}$	0.99	0.942 ± 0.005	1.89 ± 0.040
Mexico $_{naturalized}$	0.99	0.973 ± 0.004	1.90 ± 0.001
South Africa $_{planted}$	0.97	0.758 ± 0.006	1.75 ± 0.006
South Africa $_{naturalized}$	0.97	0.830 ± 0.070	1.80 ± 0.003
Native region $_{planted}$	0.99	0.971 ± 0.030	1.88 ± 0.020
Native region $_{naturalized}$	0.99	0.952 ± 0.040	1.79 ± 0.001

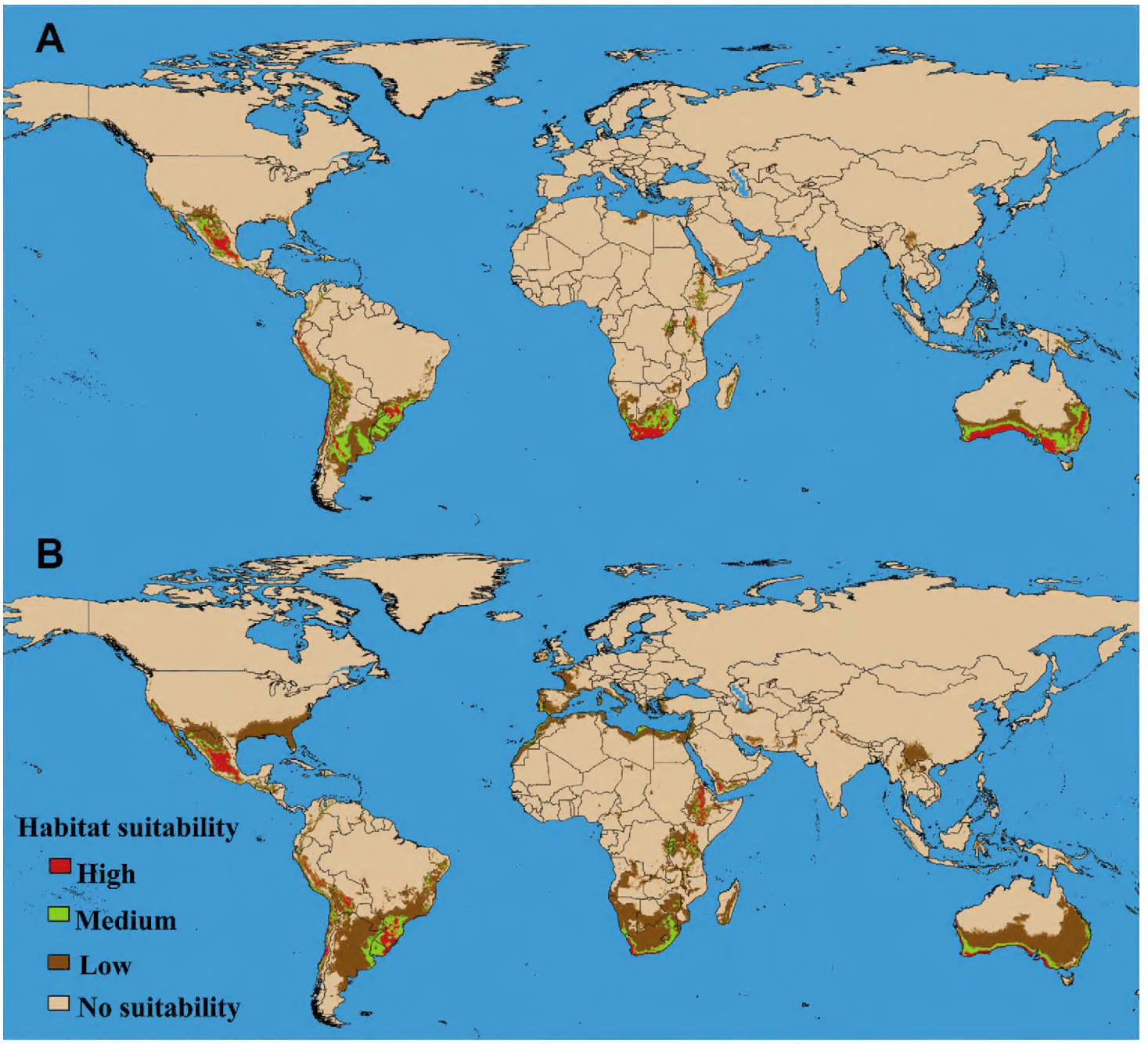

Figure 1. Global distribution model of Peruvian Peppertree (*Schinus molle* L.) with naturalized (**A**) and planted populations (**B**).

In the global models, the highest habitat suitability (> 0.60) occurred in central Mexico, the coastal regions of South Africa, some regions of eastern Africa, and the Andean Plateau of Peru and Bolivia, all of which correspond to arid and semi-arid climates (Figure 1). However, the Global $_{planted}$ model had a higher coverage, with a low and medium habitat suitability in temperate, such as Mediterranean, and arid climates (Figure 1). This was similar for the regional models of Mexico, California, Australia, and South Africa in which the largest area of suitable habitat was found from the northern to central Mexico, along the entire coast to north-central California, the southern coast and the east part of Queensland, Victoria, and New South Wales in Australia, as well as the Cape coast of South Africa (Figs 2–3, 5–6). The coverage area of habitat suitability of naturalized populations in its native region was the highest, whereas the coverage of planted populations was lower (Figure 4).

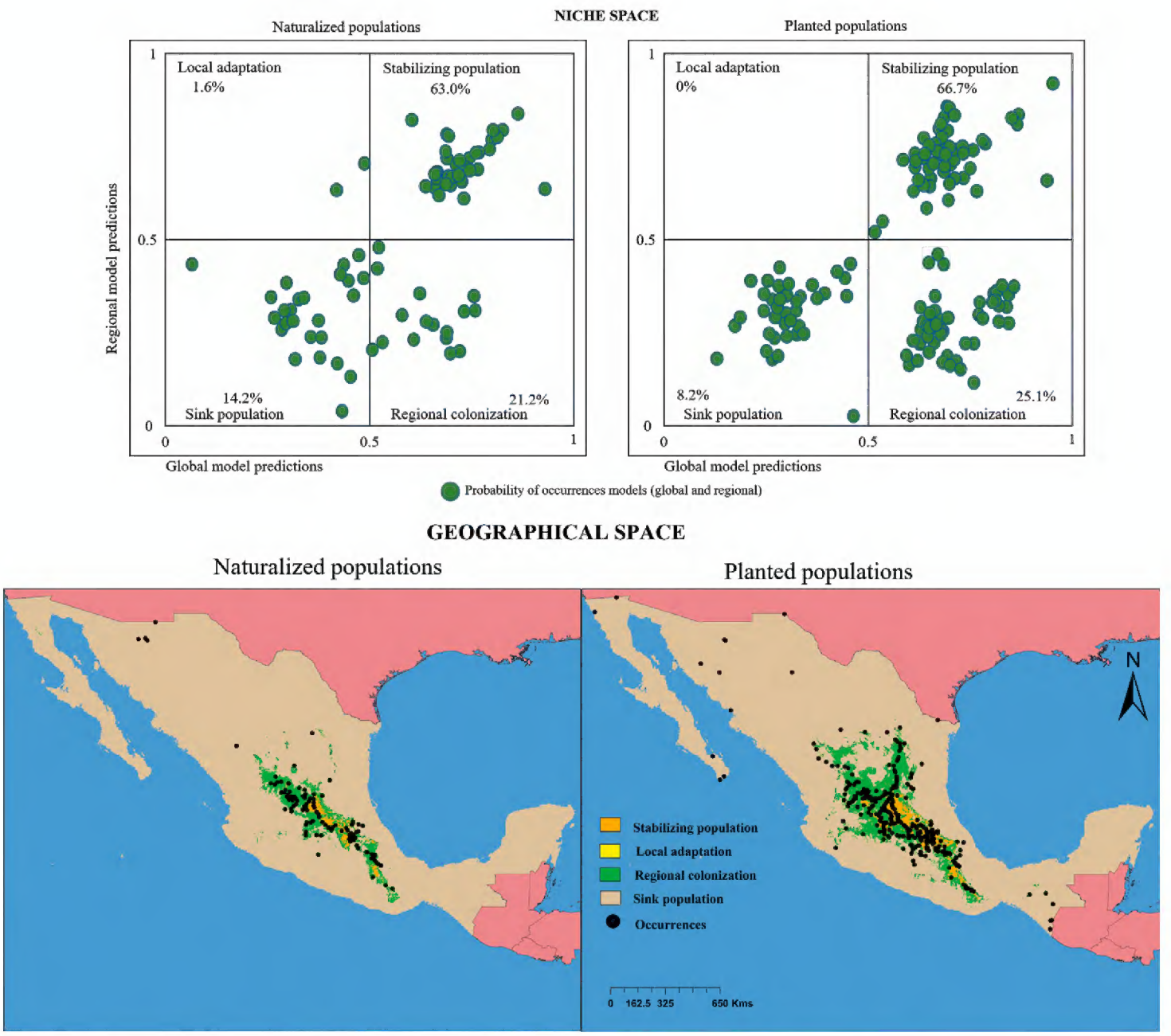

Figure 2. Invasion stages for the Peruvian Peppertree (*Schinus molle* L.) with naturalized and planted populations in Mexico.

In the niche space, the highest proportion of the predicted presences for naturalized and planted populations fell within the regions with stabilized populations (Figures 2–6). For the cases of the planted populations of Australia and South Africa, a substantial proportion of predicted presences fell within sink populations (Figures 5, 6). However, in the niche space, in the range associated with native regions, in both the naturalized and planted populations the highest proportion of predicted presences was within sink populations (Figure 4).

Discussion

The global invasion of *S. molle* suggest source-sink dynamics from the native to the invaded range, and its populations are found at different stages of invasion in Australia, California, Mexico, and South Africa. Although most *S. molle* populations are

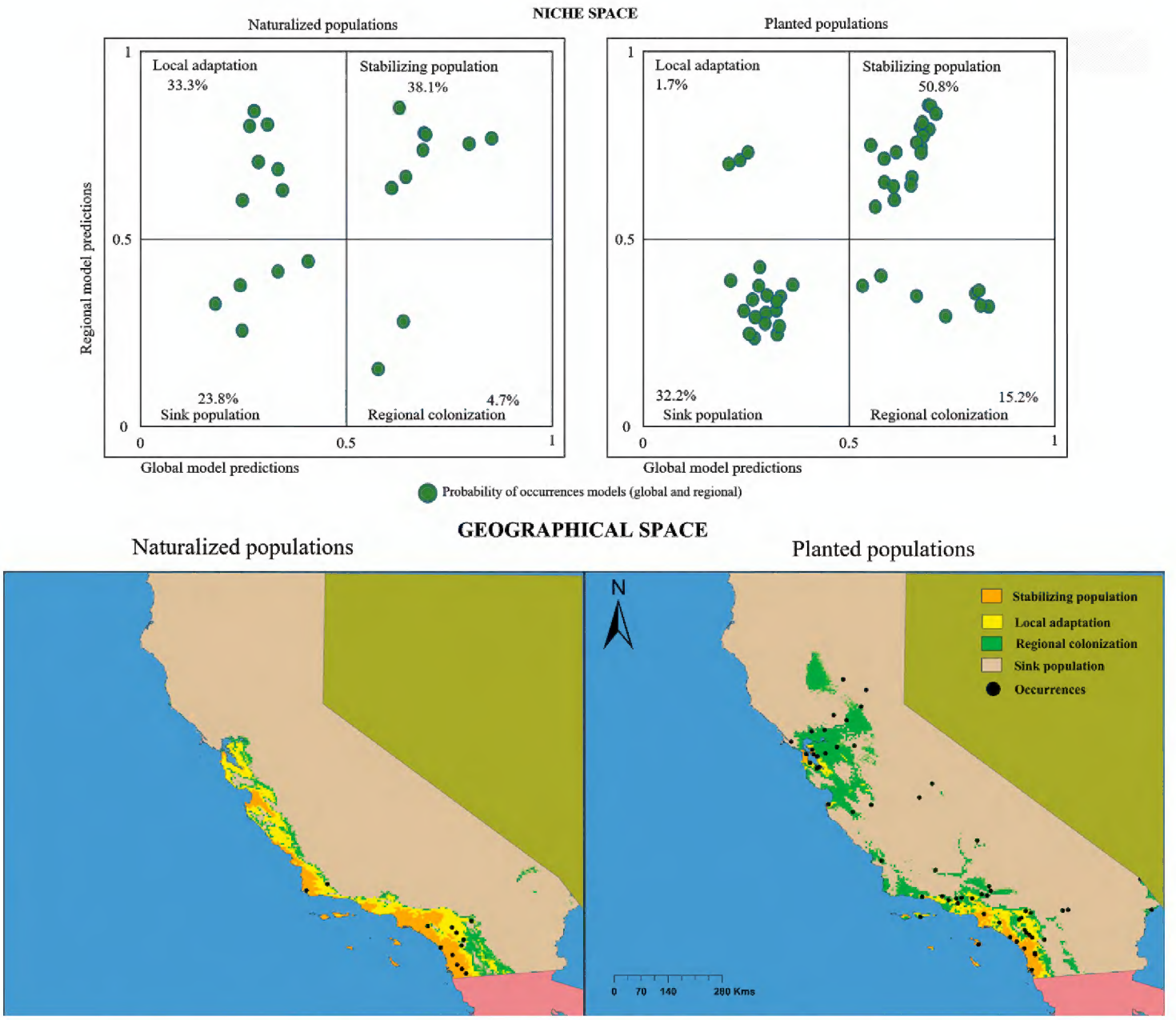

Figure 3. Invasion stages for the Peruvian Peppertree (*Schinus molle* L.) with naturalized and planted populations in California, USA.

stable, some exhibit high extinction risk (and persist as sink populations). Our findings suggest that in Mexico and California, both naturalized and planted populations of *S. molle* are stabilized, whereas only naturalized populations in natural environments of Australia and South Africa are stabilized. Our analysis allowed us to predict the regions that are most susceptible to invasion of the *S. molle* based on its climatic niche requirements. Although the invasion process is complex and different for each species, comparing global and regional climatic niches provides a useful tool that initially addresses these complexities and generates different hypotheses to be tested in future experimental studies (Taucare-Ríos et al. 2016).

In Mexico, Australia, California, and South Africa, both niche models predicted the most suitable habitats in the central part and the Mexican Plateau in Mexico, the Californian coast, the southern coast and the east part of Queensland and New South Wales in Australia, as well as the Cape coast of South Africa. Factors relating to temperature were the most important for defining the potential distribution of this species. In this regard, our results confirm those of earlier studies on *S. molle* (Iponga et al.

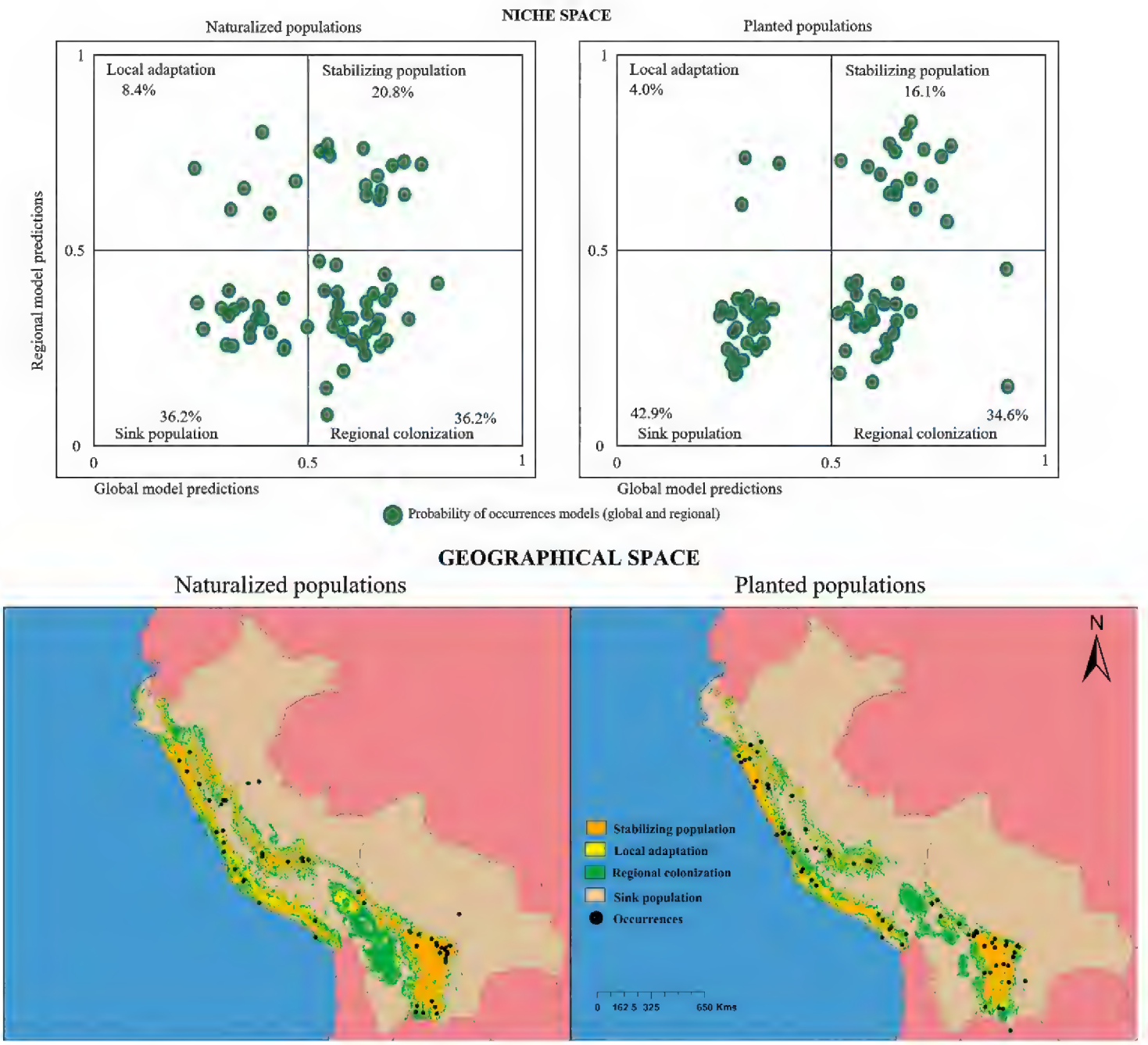

Figure 4. Invasion stages for the Peruvian Peppertree (*Schinus molle* L.) with naturalized and planted populations in South America (native region).

2008; Lemos et al. 2014, 2019; Ramírez-Albores et al. 2020; Guerra-Coss et al. 2021). *Schinus molle* can be established easily in arid and semiarid climates in Mexico, California, Australia, and South Africa, probably because of the similarities in the climate in their native range (e.g., Richardson and Thuiller 2007 [figure 2] for South Africa).

In this context, and similar to other studies (e.g., Taucare-Ríos et al. 2016), our models showed that in regions with longer residence times (i.e., longer time elapsed since the first record), the number of stable populations increases, while the regional colonization remains low. This suggests that the species' current distribution is not limited primarily by abiotic factors, but instead reflects human aid in facilitating the expansion of this highly invasive species beyond its climatic thresholds. When comparing the native niche model with the global niche model, the ecological requirements of *S. molle* are maintained despite the climatic differences; in other words, the populations show niche conservatism in the invaded regions. In the regional models, *S. molle* populations appear to occupy new niches, which may be facilitated by human actions such

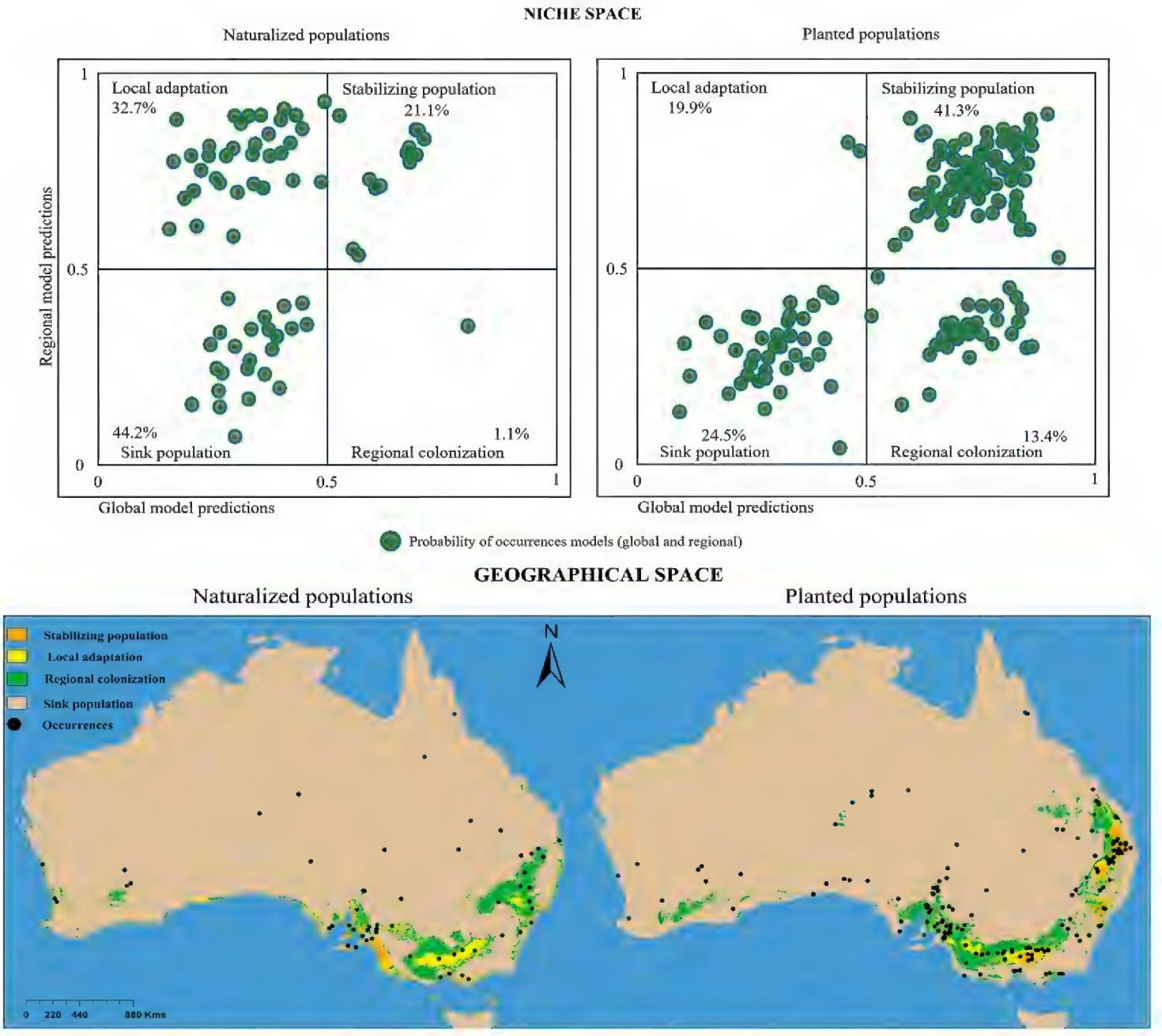

Figure 5. Invasion stages for the Peruvian Peppertree (*Schinus molle* L.) with naturalized and planted populations in Australia.

as irrigation, which generates new environments favorable to the species even though the natural climate is outside the species' niche (Taucare-Ríos et al. 2016, 2018).

Although the range-filling analysis showed that the naturalized and planted populations in these regions may still colonize more suitable habitats, the populations may be in equilibrium with the environment. This partial filling of the native niche in the invaded region has been reported for other invasive plants (Rouget et al. 2004; Petitpierre et al. 2012; Goncalves et al. 2014; Kolanowska and Konowalik 2014; Peña-Gómez et al. 2014) and has been documented in other studies of *S. molle* (Richardson et al. 2010; Ramírez-Albores et al. 2020). This would explain why *S. molle* has only colonized a fraction of the environments that are climatically suitable for the species. It is well known that when humans translocate species across biogeographic barriers, the introduced individuals often constitute a biased sample of the genetic variability of the populations across the entire native range (Chun et al. 2009). Therefore, invasive plants may fail to occupy the full range of climatic conditions that occur in their native niches,

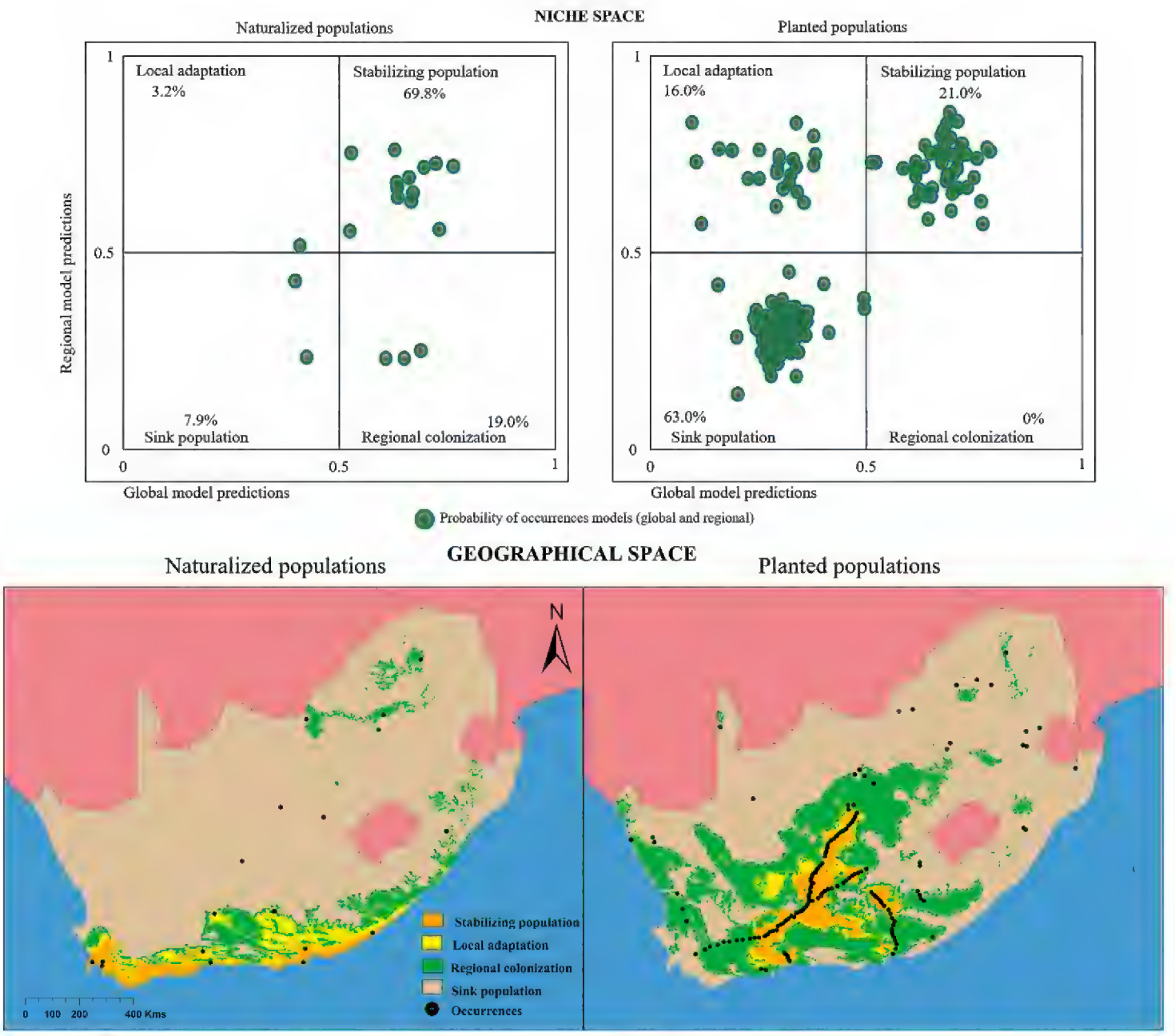

Figure 6. Invasion stages for the Peruvian Peppertree (*Schinus molle* L.) with naturalized and planted populations in South Africa.

even when these conditions are available in the invaded regions (Early and Sax 2014; Alexander 2016). There is no evidence of genetic rescue (i.e., increased genetic variability due to reintroductions) in the global history of introductions of the species. Invasive peppertrees may have experienced a genetic bottleneck because a small, random, and nonrepresentative fraction of the full niche of the species was captured when seeds were harvested in the native range. Testing this hypothesis would require comparing genetic profiles between the native and invasive peppertrees. However, *S. molle* populations in these regions probably experienced genetic bottlenecks, as often happens when alien plants are introduced into new regions (Prentis et al. 2008; Xu et al. 2015; Xia et al. 2020). On the other hand, significant genetic structure and a low levels of population genetic diversity were observed in an analysis of nine populations of natural occurrence in the Brazilian Pampa biome (Lemos et al. 2015). Thus, if multiple introductions are performed in new areas using seeds from different origins, the genetic variation can be increased since different alleles may be sampled across divergent populations.

Nonetheless, the high capacity of colonizing new areas seems to be relatively independent of the level of genetic variation of the introduced plants and of the human interference, like irrigation. Although the Incas planted and irrigated *S. molle* around palaces, temples, and public building (as it was considered a sacred tree; Mendonça-Rocha et al. 2012), irrigation does not seem to be essential for seedling establishment. In a controlled experiment in California, where the species was introduced and naturalized, seedling growth was fast through the summer regardless of the irrigation regime (Howard and Minnich 1989). The high plasticity of this species seems to be efficient in driving its capacity of introduction into and surviving in different environments (Lemos et al. 2015). This capacity has been corroborated if we consider the large number of different sites were *S. molle* was introduced and is currently naturalized, regardless of human intervention. The rate of local adaptation and populations stabilization predicted in our model suggests that planted populations in the natural occurrence range of *S. molle* (Figure 2) is similar to Mexico, California, Australia, and South Africa (Figures 3–6). Thus, local adaptation seems to be independent of human interference and can occur as a natural process for this species.

The Global $_{planted}$ model predicts large areas of suitable habitat areas in the western and Mediterranean regions of Europe and Africa, the Brazilian Atlantic coast, and the Pampa region of Argentina, Brazil, and Uruguay, showing a high proportion of stable populations and few sink populations compared to the Global $_{naturalized}$ model. This pattern is similar to that reported by Richardson et al. (2010) and Lemos et al. (2019), who mentioned that the largest areas of suitable habitat for the establishment of *S. molle* are subsidized by humans. In general, sink populations were found in tropical and cold climates as well as deserts which represent stressful and extreme temperatures. Also, in several South American countries, we found populations that had undergone regional colonization in Ecuador, Colombia, Chile, Paraguay, Brazil, and Argentina. However, *S. molle* populations in Mexico suggest that the seeds used in founder populations came from sites that cover less than 10% of the full range of climatic conditions over which this species occurs in its native region (Ramírez-Albores et al. 2016, 2020). Indeed, as far as we know, the *S. molle* was introduced in Mexico only once.

There were some areas for which local adaptation was predicted (see Figures 2–6). We suggest possible explanations for local adaptation in our naturalized niche models as the species' ability to exploit empty niches, or on account of local disturbances have created new habitats (Sax et al. 2013). Our results support the hypothesis that alien species are more successful in human-modified environments (Pyšek and Richardson 2010). Indeed, such environments can result in the creation of vacant niches that can be filled by alien species (Catford and Downes 2010). On the other hand, planted models may have overestimated the potentially suitable areas because not all predicted areas have suitable habitats for *S. molle* (e.g., tropical climates). Furthermore, occurrences in urban areas where the species may be subsidized by human activities may cause the models to overpredict suitability in nonurbanized areas with similar environmental features in other regions. Therefore, we suggest that it is plausible in this case that the geographical range of *S. molle* can be further extended as humans continue to

use this species for ornamental and forestry purposes in urban and rural environments, thereby modifying the fundamental niche of *S. molle* (Ingeloff et al. 2017; Qiao et al. 2017). However, this could also be established by natural processes as it occurs in the Brazilian Atlantic coast and the Pampa region (Lemos et al. 2014, 2019).

Conclusions

The invasion stages of *S. molle* vary across regions in its adventive range; this is the result of the complex interplay of stochastic factors and abiotic and biotic mediators. Residence time as well as climatic and anthropic factors have contributed to the success of *S. molle* populations. This study provides a preliminary approach for understanding the process of invasion by this invasive tree, thereby helping to elucidate the dimensions of the "invasion debt" (*sensu* Rouget et al. 2015) that clearly exists for *S. molle* in many areas. Such insights will be crucial for developing strategies for the management of this important invasive tree to avoid or at least reduce its future impacts in recipient ecosystems.

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Supplementary material 1

Table S1

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Data type: Databases consulting

Explanation note: Databases consulted in collating occurrence records of Peruvian Peppertrees (*Schinus molle* L.).

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